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A new groenlandaspidid arthrodire (Pisces; Placodermi) from the Middle Devonian Aztec Siltstone, southern Victoria Land, Antarctica

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Abstract — *Boomeraspis goujeti* gen. et sp. nov is described from isolated trunk-shield plates found in the basal 30 metres of Aztec Siltstone exposed at Alligator Peak in the Boomerang Range of southern Victoria Land. *Boomeraspis* is characterised by its broad posterior dorsolateral plate (PDL) which has an inflected main lateral line canal and a strongly convex dorsal margin, and the posterior lateral plate (PL) features a strong lateral ridge. These features place *Boomeraspis* as a primitive member of the family Groenlandaspididae, distinguished from both *Tiaraspis* and *Groenlandaspis* by its proportionately longer PDL, strongly ridged and larger PL, and also by the long posterior division of the ventral lamina on the PVL plate.

INTRODUCTION

Devonian fossil fish remains were first collected from southern Victoria Land, Antarctica, in the summer of 1911–12 by Mr Frank Debenham, a member of Scott's "Terra Nova" expedition. His finds near Granite Harbour came from moraine material, and were later described by Woodward (1921), who correctly assigned a Devonian age to the small assemblage of fish scales, teeth and fragmentary bones. The first extensive collections were made *in situ* by B. M. Gunn and G. Warren during the 1955–1958 Transantarctic Expedition. More extensive collections of fossil fish were made in the summer of 1968–69 by members of the Victoria University of Wellington Antarctic Expeditions (VUWAE 13). Dr Alex Ritchie, of the Australian Museum, and Dr Gavin Young, Australian Geological Survey Organisation, made extensive collections of the Aztec Siltstone fishes over the summer of 1970–71 as part of VUWAE 15. White (1968) had described the fish remains collected by Gunn and Warren, and Ritchie (1972) summarised the distribution of the Aztec Siltstone fish faunas found on VUWAE 13, and later described the arthrodire *Groenlandaspis antarcticus* from the 1970–71 collection (Ritchie 1975). Young (1982,1988,1989a) has since described sharks, bothriolepid antiarchs and culmacanthid acanthodians, Young *et al.* (1992) have monographed the crossopterygian fauna, and Turner and Young (1992) have described the thelodonts. The Aztec Siltstone is now known to contain over 30 species of fossil fishes, making it one of the most diverse freshwater fish faunas of its age, and a keystone to biostratigraphic correlations within the East Gondwana Province (Young 1989b,1993).

During the 1988/89 season Woolfe *et al.* (1990) discovered fish-bearing Aztec Siltstone in the Cook Mountains, nearly 100 km south of the previously known sites. In the 1991/92 season the author joined M. Bradshaw, F. Harmsen and B. Staite in an expedition to collect fossil fish material from the Cook Mountains, and revisit known sites in the Skelton Névé region. It will be several years before the vast amount of new material collected from that expedition is prepared and ready for description. This paper describes a new groenlandaspidid arthrodire based on a few isolated plates recovered from the southeastern spur of the Alligator Ridge region of the Boomerang Range (site 21, of Young 1988, Fig. 1). Other undescribed phlyctaeniid arthrodires are known from the Aztec Siltstone (e.g. Young 1991) although the material described here can be readily distinguished from these forms by showing features characteristic of the family Groenlandaspididae. Although two scant fish faunas have been reported from the higher units in section 21, the material described herein came from a lower fish-bearing horizon within the basal 30 metres of the Aztec Siltstone which may be identical with the fossiliferous horizon mentioned by Barrett and Webb (1973, section 3, as approximately 32 metres above the base of the unit) but not collected by them or by subsequent expeditions. All specimens are reposited in the collections of the Western Australian Museum (WAM).

Abbreviations used in the text and figures are: ADL, anterior dorsolateral plate; AL, anterior lateral plate; AVL, anterior ventrolateral plate; llc, main lateral-line canal groove; MD, median dorsal plate; ov.ADL, surface overlapped by ADL plate; ov.AL, area overlapped by AL plate; ov.MD, area overlapped by MD plate; ov.PL, area overlapped by PL plate; ov.PVL, area overlapped by PVL plate; PDL, posterior dorsolateral plate; PL, posterior lateral plate; PVL, posterior ventrolateral plate; ri,

ridges; Sp, spinal plate; tr.r, transverse ridge on lateral lamina of trunk-shield;

SYSTEMATICS

Order Arthrodira Woodward, 1891

Suborder Phlyctaenioidei Miles, 1973

Infraorder Phlyctaenii Miles, 1973

Family Groenlandaspididae Obruchev, 1964

Boomeraspis gen. nov.

Type species

Boomeraspis goujeti sp. nov.

Diagnosis

A groenlandaspidid arthrodire having a PDL which has an externally ornamented surface approximately as long as high, with a prominent vertical ridge developed ventral to the point of

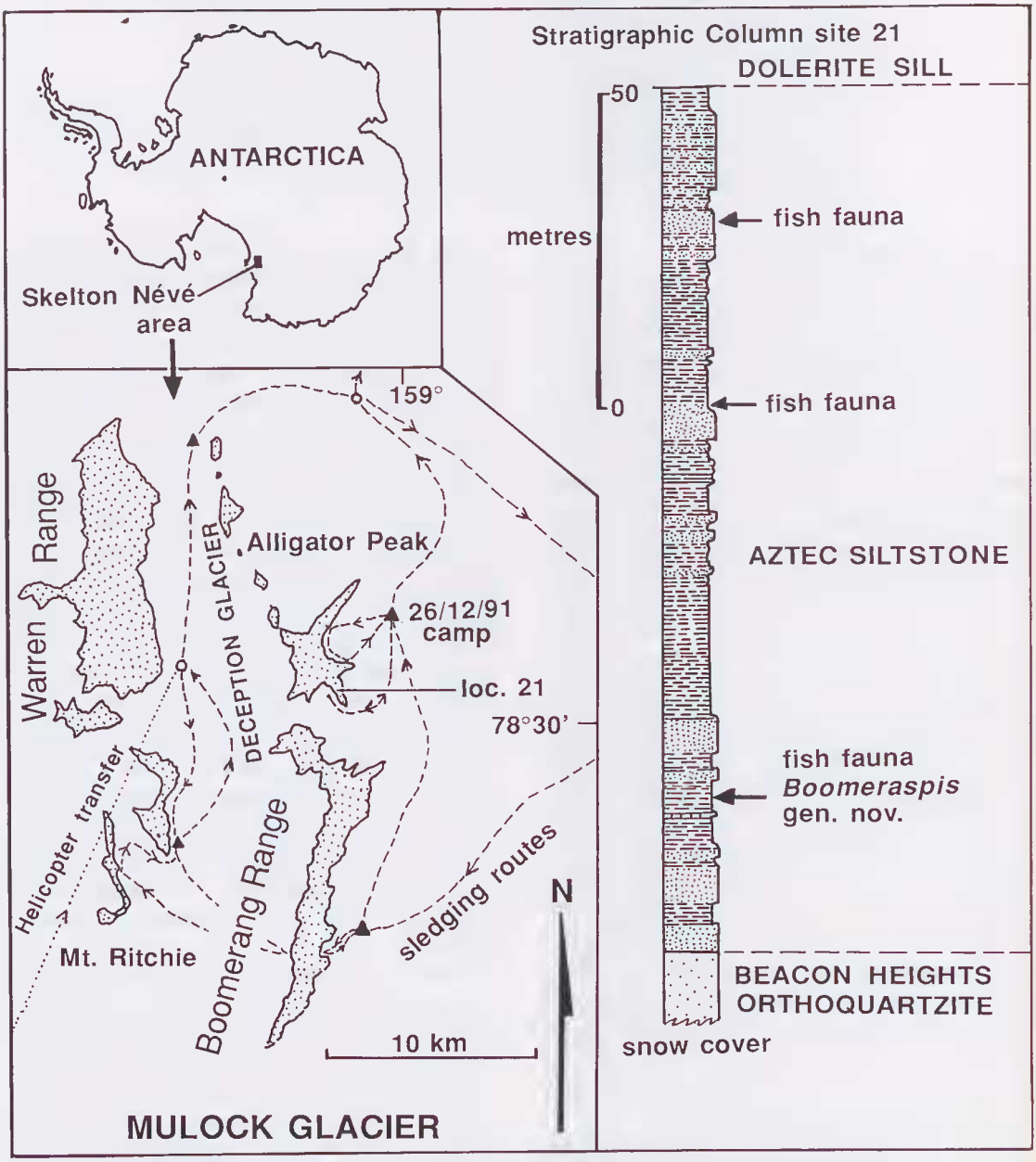

Figure 1 Locality map and stratigraphic section (after Young 1988) showing where the type collection of *Boomeraspis* material was found.

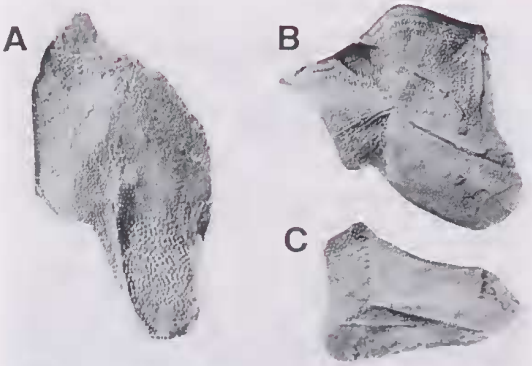

Figure 2 *Boomeraspis goujeti* gen. et sp. nov. A, paratype right PVL plate, WAM 93.7.4.; B, holotype right PDL plate, WAM 93.7.2; C, paratype right PL plate, WAM 93.7.3; All are latex peels whitened with ammonium chloride, x1.5.

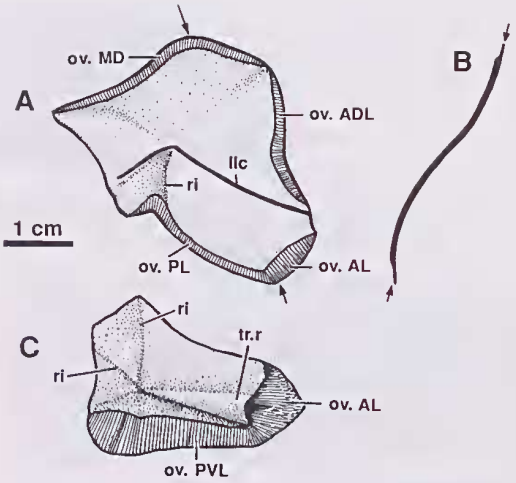

Figure 3 *Boomeraspis goujeti* gen. et sp. nov. A, B, right PDL plate, WAM 93.7.2 (holotype). A, lateral view; B, cross-sectional shape of external surface as indicated on A (internal surface unknown). B, right PL plate in lateral view (paratype WAM 93.7.3).

inflection on the main lateral-line canal groove; PL has a prominent transverse ridge which becomes deeper anteriorly. Ornament on the PDL is of vertically directed rows of fine tubercles near the dorsal margin.

Remarks

Although known from only fragmentary material *Boomeraspis* is referred to the Groenlandaspididae because of the highly convex dorsal margin and inflected main lateral line canal on the PDL plate. It differs from the only other two known members of the family by its proportionately larger, strongly ridged PL plate, and the fact that the PDL is more elongated rostrocaudally compared with the narrow, higher PDLs seen in *Groenlandaspis* and *Tiaraspis*. The trunk plates described here are not considered likely to belong to *Antarctaspis* White 1968 because this genus has been referred to as a stem-group phyllolepid (Long 1984; Young 1991) and, based on these cranial similarities, the corresponding trunk-shield would be expected to be quite unlike that of groenlandaspidid arthrodires. Nor is *Boomeraspis* likely to be confused with *Antarctolepis* White, 1968 because the single plate of that genus, an AL, lacks a prominent lateral ridge that would be present on the AL of *Boomeraspis* as it has a prominent lateral ridge running anteriorly off the PL plate. Ritchie (1975) notes that *Antarctolepis* appears quite distinct in its AL plate from that of *Groenlandaspis*, and is therefore not likely to be confused with other members of that family.

Etymology

The generic name is after the locality (Boomerange Range) and the Greek "aspis" meaning "shield".

Boomeraspis goujeti sp. nov.

Figures 2–5, 6B

Diagnosis

Same as for genus.

Type material

Holotype WAM 93.7.2, an impression of the external surface of a complete right PDL plate (Figures 2B; 3A, B). Paratypes WAM 93.7.3, a complete right PL plate (part and counterpart; Figures 2C, 3C); WAM 93.7.4, a complete right PVL plate (part and counterpart; Figure 2A); WAM 93.7.5, an incomplete posterior division of a spinal plate (mostly impression only; Figure 4).

Etymology

The species name is for Dr Daniel Goujet of the Musée d'Histoire naturelle in Paris, for his contributions to arthrodire studies.

Locality and age

The specimens all come from a dark green laminated mudstone occurring immediately above the first thick bluff-forming sandstone unit, approximately 30 metres from the base of the Aztec Siltstone exposed along the southeastern spur of Alligator Ridge (locality 21 of Young 1988). All the specimens were found close together in loose slabs of mudstone scree on top of the outcrop. As all the plates are from the right side, and are of correct size to fit together, it is quite possible that they are

Figure 4 *Boomeraspis goujeti* gen. et sp. nov. Sp plate, as preserved. Camera lucida sketch; where the bone is missing the impression of the tubercular ornament in the rock is indicated, paratype WAM 93.7.5.

from the same individual. The unit from which the fish plates were collected also contains isolated thelodont scales of *Turinia antarctica*, and plates of an as yet undetermined species of *Bothriolepis*. *Boomeraspis* therefore comes from within either the *askinae* or *kohni* biozones of Young (1988), and could be regarded as late Givetian in age.

Description

The four isolated plates of *Boomeraspis* (Figures 2–4) may be used to give a tentative restoration of the overall shape of the trunk-shield (Figure 5), which assumes it was short and relatively high as in other groenlandaspidids. The trunk-shield had a prominent lateral ridge running from the PL plate which presumably continued on to the AL plate, as for other phlyctaeniids, such as *Tiaraspis* (Gross 1962, Schultze 1984) and *Phlyctaenius* (Young 1983).

Posterior dorsolateral plate

The PDL (Figures 2A; 3A, B) measures 30 mm in rostrocaudal length along the dorsal margin, and is 42 mm in maximum depth as measured from the top of the dorsal margin to the anteroventral overlap area dividing the PL and AVL plates. The dorsal margin of the PDL tapers vertically (Figure 3B) suggesting that the two PDLs most likely met in contact underneath the MD plate as occurs in *Groenlandaspis*. The main lateral-line canal groove (llc, Figure 3A) is inflected through an angle of 120° in the posterior third of the plate, and there is a prominent vertical ridge (ri, Figure 3A) running from the point of inflection to the ventral margin of the plate. The posterior division of the main lateral-line canal is less well defined and does not extend all the way to the posterior margin of the plate. The ADL overlaps the PDL (ov.ADL, Figure 3A) for about two thirds the anterior margin, but does not overlap that section of the PDL containing the anterior end of the main lateral line canal groove. The overlap margins for the MD, ADL and PL plates (ov.MD, ov.ADL, ov.PL; Figure 3A) are slightly narrower than that for the AVL plate (ov.AL, Figure 3A). The inner surface of the PDL is not known.

Posterior lateral plate

The PL is a relatively large and distinctive plate in *Boomeraspis* compared to that in other groenlandaspidids (Figure 6), extending for nearly the length of the PDL plate. It has a subrectangular outline with a strongly convex dorsal margin (Figures 2C, 3C), and a gently curved posterior margin that is oriented almost vertically. The prominent lateral ridge (tr.r, Figure 3C) originates in the posterior third of the plate and increases in thickness evenly towards the anterior margin, appearing as a thick ridge on the lateral lamina. The ventral external margin of the PL (where the dermal ornament terminates) is almost straight, and the overlap areas for the PVL and AL (ov.PVL, ov.AL, Figure 3C) are both quite extensive, much broader than the overlap margins on the PDL plate. Unlike *Groenlandaspis* the PL of *Boomeraspis* lacks a posteroventral extension of the overlap area for the PVL plate. The ornament is of regularly spaced tubercles which are largest in the posterodorsal corner of the plate.

Posterior ventrolateral plate

The PVL (Figure 2A) is known from part and counterpart, although the anterior margins are not well preserved. It is a narrow plate having a lateral lamina extending just over half the plate length. The posterior margin of the lateral lamina is evenly

Figure 5 *Boomeraspis goujeti* gen. et sp. nov. Attempted restoration of the trunk shield based on the presence of the PVL, PL, PDL and Sp plates and their margins with neighbouring plates. Extent of the anterior trunk-shield plates and shape of the MD plate is based on comparsions with other groenlandaspidids.

curved, meeting the ventral lamina along a prominent ventrolateral ridge. This ridge is only present in the posterior half of the plate. A less prominent, but still well-defined ridge is developed from the anterodorsal corner of the lateral lamina running posteroventrally towards the ventrolateral ridge, but tapering out well before reaching it. A small section of the overlap area for the AL plate is preserved, indicating that an extensive overlap was developed between the two plates. The ornament of the PVL consists of very fine, small tubercles for most of the plate, with larger, coarse tubercles present on the posterior half of the ventral lamina. The PVL differs from that of *Groenlandaspis* and *Tiaraspis* in its narrower ventral lamina and presence of a weak ridge running posteroventrally from the anterior corner of the lateral lamina.

Spinal plate

The Sp plate is almost completely preserved, missing only a section of the anterior region. It shows small pointed tubercles along the lateral margins and a row of slightly larger, recurved tubercles lining part of the the mesial edge that protected the lateral edge of the pectoral fin. The bone is absent from most of the surface of the Sp, but impressions of the ornament show rows of aligned tubercles covered the external surface. In general form it is quite similar to the Sp in *Groenlandaspis* (Ritchie 1975).

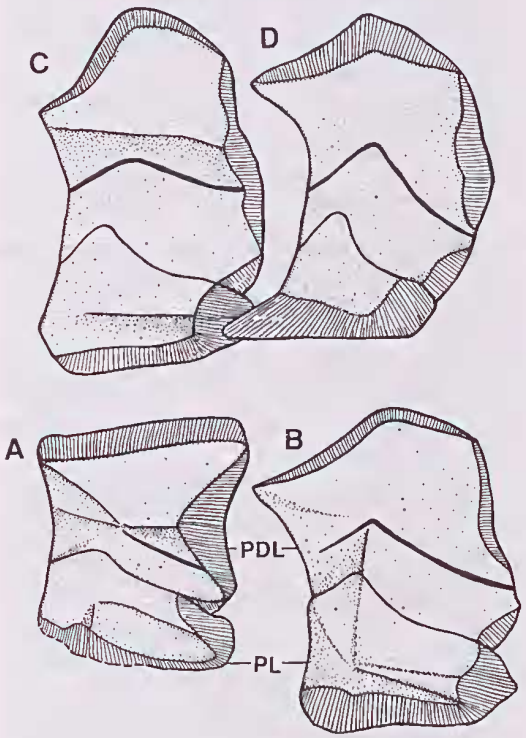

Figure 6 Comparison of right PDL and PL plates of A, *Phlyctaenius stenosus* (after Young 1983); B, *Boomeraspis goujeti* gen. et sp. nov.; C, *Tiaraspis subtilis* (modified after Gross 1962, and Schultze 1984), and D, *Groenlandaspis antarcticus* (after Ritchie 1975). Not to scale.

PHYLOGENETIC POSITION OF *BOOMERASPIS*

Boomeraspis is placed within the family Groenlandaspididae because of its deep PDL plate which has a strongly inflected main lateral-line canal groove and a well-rounded, convex dorsal margin (Ritchie 1975, Goujet 1984). Although the inner surface of the PDL is unknown, the cross-sectional shape of the external surface is very similar to that of *Groenlandaspis* and suggests that it is likely that the two PDLs either met in dorsal contact or were closely situated under a high MD plate. Within the Groenlandaspididae only three genera are currently known, although others have been recognised and are currently being studied from the Early-Middle Devonian Mulga Downs Group of New South Wales by Dr Alex Ritchie (Ritchie 1975, p.571 "a new undescribed form from the Mulga Downs Group"). Clearly to resolve the question of whether *Boomeraspis* is more closely related to *Groenlandaspis* or to *Tiaraspis* depends largely on finding more complete remains, especially the head-shield.

The primitive condition in all phlyctaeniids, based on the Early Devonian species from Spitsbergen and Canada (Goujet 1984, Young 1983), is to have an elongate trunk-shield which has very long PL and PDL plates, and the PDL carries a straight lateral-line canal groove. The PL plate in most primitive phlyctaeniids may have a well-developed lateral ridge present (e.g., *Phlyctaenius*; Young 1983; arctolepids, arctaspids; Goujet 1984). Comparisons of the trunk-shield morphology would suggest that *Boomeraspis*, by having relatively longer PDL and PL plates, and a ridge on the lateral lamina of the PL plate, is more plesiomorphic than either *Tiaraspis* or *Groenlandaspis*. *Groenlandaspis* is considered more derived than *Tiaraspis* and *Boomeraspis* in having a PL plate that lacks any lateral ridge and has a well-developed, posteriorly-directed overlap surface for the PVL plate. The only synapomorphy that seems to unite *Boomeraspis* with either *Tiaraspis* or *Groenlandaspis* is the shape of the dorsal margin of the PDL plate, which in *Groenlandaspis*, and apparently (assumed in *Boomeraspis*) meets the opposing PDL underneath the MD plate. Both Ritchie (1975) and Schultze (1984) used this feature as an autapomorphy of the genus *Groenlandaspis*, so its suggested presence in *Boomeraspis*, based on

the external form of the PDL (Figure 3B), would support a sister-group relationship to *Groenlandaspis*.

The groenlandaspidid arthrodires range from the Early Devonian (Siegennian-Early Emsian) of Germany (*Tiaraspis subtilis*) to the very end of the Devonian (*Groenlandaspis*, Givetian-late Famennian, Antarctica, Australia, Middle East; Janvier and Ritchie 1977; Famennian of the East Greenland and Europe; Ritchie 1975), and possibly the Lower Carboniferous of Turkey (Janvier *et al.* 1984). The presence of several undescribed groenlandaspidids in the Early-Middle Devonian Mulga Downs Group of New South Wales and of several species of *Groenlandaspis* in the Givetian Aztec Siltstone (Dr A. Ritchie pers. comm. 1993) would suggest that the East Gondwana Province was a centre of radiation for the groenlandaspidids, immediately following the Gondwana origin for the group sometime in the Early Devonian (Germany may have then part of the northern margin of Gondwana; Young 1987a, 1987b). Although most groenlandaspidids occur in freshwater red-bed or alluvial sequences, the presence of one ADL plate of *Groenlandaspis* sp. (WAM 91.4.35) in the bedded marine limestones of the lower Frasnian Gneudna Formation, Carnarvon Basin, Western Australia, shows that the genus was capable of dispersal by marine routes.

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